Towards a revision of *Lejeunea* (Lejeuneaceae) in Malaysia

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ABSTRACT. As currently delimited, *Lejeunea* Lib. is characterised by the hyaline papilla at the proximal side of the first tooth of the lobule; the usual absence of ocelli in the leaf lobe; lobules occasionally reduced and with a single tooth; small, finely granular or homogeneous oil bodies; underleaves without or with straight, upright lobes; thin-walled epidermal cells that are larger than the medullary cells; branches of the *Lejeunea*-type; and gynoecia with lejeuneoid innovations. In Malaysia, 29 species of *Lejeunea* have hitherto been recognised. In the framework of an ongoing taxonomic revision, all characters used to circumscribe the genus and the species from Malaysia have been critically assessed based on study of fresh material collected during many field excursions throughout Malaysia (the Peninsular, Sabah, Sarawak) as well as study of herbarium material. Some characters which were neglected previously, such as the morphology of the first lobule tooth, superior central cells and female bracts and bracteoles, are being critically evaluated. These characters may be useful for differentiating *Lejeunea* from closely related genera, whereas characters of oil bodies, the perianth, the lobule with a large disc cell, and underleaves with two large basal cells, are also useful for distinguishing some species within the genus.

Keywords. *Lejeunea*, Lejeuneaceae, liverworts, Malaysia, taxonomy

Introduction

The pantropical genus *Lejeunea* Lib. is one of the largest genera in the liverwort (Marchantiophyta) family Lejeuneaceae, containing some 150–200 species, almost half of which occur in tropical Asia. The definition of the genus has long been problematic and many species currently placed in *Lejeunea* were previously assigned to other genera. It is also one of the most difficult and poorly understood hepatic genera. Species of *Lejeunea* are small to medium-sized plants, delicate, translucent, with shiny leaves in the field, frequently growing closely appressed on bark, living leaves and other substrates. The highly variable species *L. flava* has an almost worldwide distribution, occurring in Europe, North and South America, Africa, China, Japan, Indomalesia, Australasia and the Pacific region, while other species are restricted only to Asia, Europe, Africa or the Americas.

In Malaysia, 29 species of *Lejeunea* have been reported, most of them from Mount Kinabalu with 26 recorded species (Eifrig 1937; Mizutani 1963, 1966, 1970, 1978; Kodama 1976; Lee et al. 2010a). Eleven species are recorded from Peninsular Malaysia, viz., *L. anisophylla* Mont. [= *L. borneensis Steph.*] (Kitagawa 1971), *L. flava* (Sw.) Nees, *L. patersonii* (Steph.) Steph., *L. cuculliflora* (Steph.) Mizut. [=*Taxilejeunea cuculliflora* Steph.], *L. albescens* (Steph.) Mizut. [= *Taxilejeunea albescens* Steph.] (Inoue 1967), *L. lumbricoides* (Nees) Nees, *L. umbilicata* (Nees) Nees (Tixier 1980), and *L. patriciae* Schäf.-Verw. (= *L. pilifera* Tixier) (Schäfer-Verwimp 2001), *L. discreta, L. eifrigii,* and *L. sordida* (Lee et al. 2010b). A revision of the genus *Lejeunea* in Malaysia is currently being undertaken at Universiti Kebangsaan Malaysia by the first author, based on examination of herbarium materials collected from this country, mainly by Mizutani in the twentieth century (Mizutani 1966), and also specimens from other herbaria such as SING, BOHR, HIRO, BO, CAL as well as fresh materials collected by the first author. Named specimens from adjacent countries are being compared with the Malaysian taxa. Approximately 500 samples, including most of the type specimens of *Lejeunea* occurring in this country, have so far been examined. The type specimens are from the Conservatoire et Jardin botaniques de la Ville de Genève (G), Switzerland, Herbarium Haussknecht (JE), Germany, and the Hattori Botanical Laboratory (NICH), Japan.

Characters delimiting the genus

Characters that differentiate the genus *Lejeunea* from others include the hyaline papilla at the proximal side of the first tooth of the lobule; the usual absence of ocelli; small, finely granular or homogeneous oil bodies; occasionally reduced lobules with one tooth; underleaves that are entire or with 2 straight, upright lobes; branches of the *Lejeunea*-type; and gynoecia with lejeuneoid innovations. Furthermore, there are some additional characters that appear to be useful in defining the genus and which were neglected previously, such as the morphology of the first lobule tooth, superior central cells and female bracts and bracteoles.

First tooth. The first tooth in most species of *Lejeunea* is straight and the apex never acuminate (Fig.1). The position of first tooth is usually upward-pointing, sometimes pointing towards the stem or away from the stem. This character can be used to distinguish *Lejeunea* from other genera in Lejeuneaceae such as *Cheilolejeunea* (Spruce) Schiffn. and *Drepanolejeunea* (Spruce) Schiffn. where the first tooth is strongly falcate and the apex occasionally acuminate, but seldom straight. *Cheilolejeunea* may sometimes be confused in its habit with *Lejeunea*, especially in the field. The main characters that differentiate these two genera are the position of the hyaline papilla and the morphology of the oil bodies. However, the hyaline papilla is often collapsed and the oil bodies rapidly evaporated in dried material. Therefore, the above described difference in the shape of the first tooth may be used to separate these two genera, at

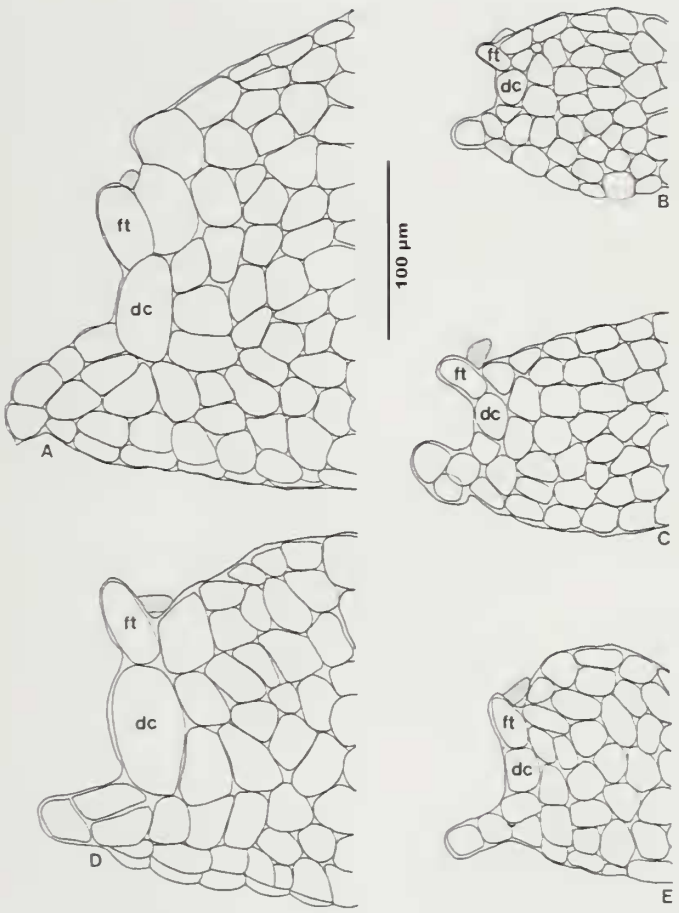

Fig. 1. Lobule apex in some Malaysian species of *Lejeunea* (hyaline papilla shown in gray). **A.** *L. discreta* Lindenb. from *Damanhuri s.n.* (UKMB). **B.** *L. microloba* Taylor from *Kodama 40783* (NICH). **C.** *L. sordida* (Nees) Nees from *G.E. Lee 1182* (UKMB). **D.** *L. lumbricoides* (Nees) Nees from *G.E. Lee 1155* (UKMB). **E.** *L. albescens* (Steph.) Mizut. from *G.E. Lee 1157* (UKMB). ft: first tooth, dc: disc cell.

least in Malaysia. The characters of the lobule tooth in Lejeuneaceae are discussed in detail by He (1996).

Superior central cells. The anatomy of the underleaf base has been discussed as a significant character in the taxonomy of the Lejeuneaceae (Bischler 1969, Winkler 1970, Gradstein 1975). The number of the superior central cells seems to be very constant at the genus level and taxonomically relevant (Gradstein 1975). The superior central cells can be perceived through transverse section of the underleaf base. The origin of the superior central cells remains uncertain (Gradstein 1975); according to Winkler (1970), they belong to the underleaf. According to Bischler (1969) and Winkler (1970), there are two superior central cells in the genera of Lejeuneoideae

(including *Lejeunea*). However, our studies show the presence of 4 superior central cells in *L. lumbricoides* (Nees) Nees, *L. eifrigii* Mizut., *L. discreta* Lindenb. and *L. sordida* (Nees) Nees (Fig. 2). This character can distinguish some *Lejeunea* species from *Drepanolejeunea,* which has only two superior central cells (Gradstein 1975).

Female bracts and bracteoles. All the female bracts of *Lejeunea* have a rather short and straight keel, and always without any wing on the keel. The margin of the bracts and bracteoles are usually entire or slightly crenulate and seldom serrulate. The absence of winged bracts in *Lejeunea* can be used to separate *Microlejeunea* where the latter usually has winged or sinuate-dentate keels, with bracts and bracteoles occasionally dentate (Schuster 1980).

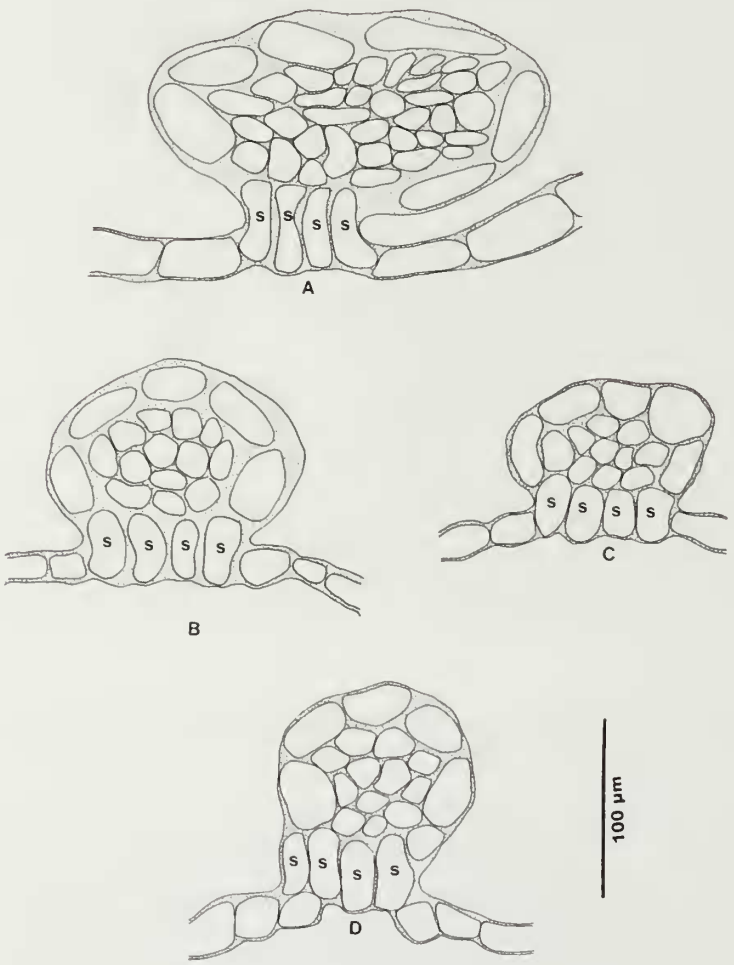

Fig. 2. Stem in cross section at the base of the underleaf, showing four superior central cells (s). **A.** *L. lumbricoides* (Nees) Nees from *G.E. Lee 1428* (UKMB). **B.** *L. discreta* Lindenb. from *Damanhuri s.n.* (UKMB). **C.** *L. sordida* (Nees) Nees from *G.E. Lee 1442* (UKMB). **D.** *L. eifrigii* Mizut. from *G.E. Lee 1194* (UKMB).

Characters in species delimitation

Leaf habit and shape. Most of the species of *Lejeunea* have flat leaves when moist, however some are with strongly convex leaves when moist, e.g., *L. pectinella* Mizut., *L. umbilicata* (Nees) Nees , *L. lumbricoides* (Nees) Nees, *L. contracta* Mizut. and *L. kinabalensis* Mizut. (Fig. 3). The convex leaf in the moist condition only seems to appear in more robust species of this genus. This character can be used to separate *L.*

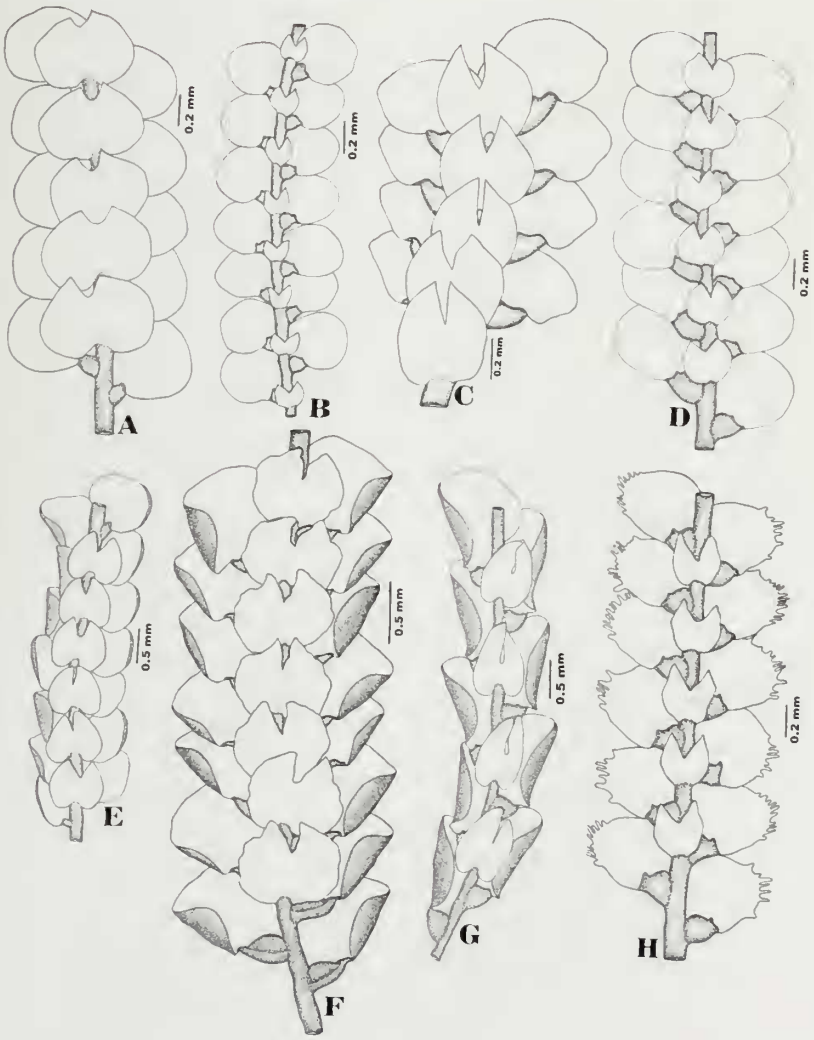

Fig. 3. Leaf habit and shape. **A.** *L. sordida* (Nees) Nees from *G.E. Lee 1154* (UKMB). **B.** *L. micholitzii* Mizut. from *Z. Iwatsuki 1383a* (NICH). **C.** *L. discreta* Lindenb. from *G.E. Lee 1146* (UKMB). **D.** *L. alata* Gott. from *G.E. Lee 1199* (UKMB). **E.** from the holotype of *L. kinabalensis* Mizut. (NICH). **F.** *L. pectinella* Mizut. from *G.E. Lee 1037* (UKMB). **G.** *L. lumbricoides* (Nees) Nees from *G.E. Lee 1155* (UKMB). **H.** *L. patriciae* Schäf.-Verw. from *G.E. Lee 1099* (UKMB).

pectinella Mizut. from *L. discreta* Lindenb., the former usually having convex leaves when moist (Fig. 3). Leaf shape in *Lejeunea* varies from narrowly to broadly ovate to rounded. The base is often gradually narrowed to the insertion which forms a long, J-shaped outline, along 10–15 cells. The apex is usually acute to rounded (Fig. 4), rarely apiculate except in *L. eifrigii* Mizut. and *L. microloba* Taylor, and without the marginal rhizoids as in *L. patriciae* Schäf.-Verw., which has leaves with 5–10 short rhizoids protruding from the apical margin.

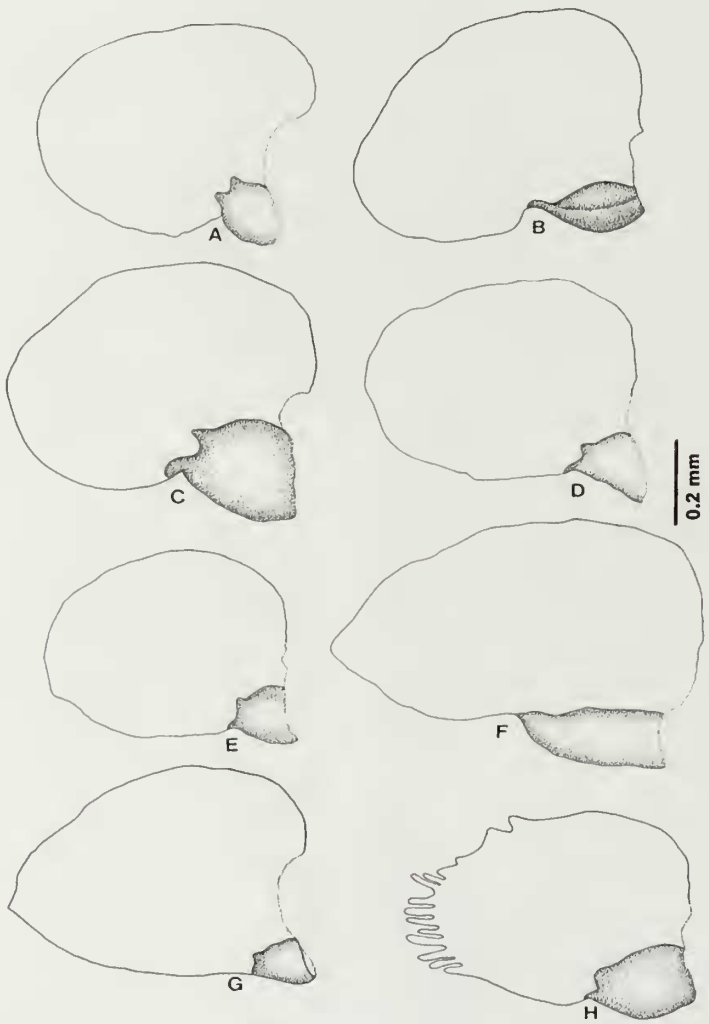

Fig. 4. Leaf morphology. **A.** *L. sordida* (Nees) Nees from *G.E. Lee 1154* (UKMB). **B.** *L. pectinella* Mizut. from *G.E. Lee 1037* (UKMB). **C.** *L. wightii* Lindenb. from *G.E. Lee 1183* (UKMB). **D.** from the holotype of *L. kinabalensis* Mizut. (NICH). **E.** *L. anisophylla* Mont. from *G.E. Lee s.n.* (UKMB). **F.** *L. discreta* Lindenb. from *G.E. Lee 1146* (UKMB). **G.** *L. eifrigii* Mizut. from *G.E. Lee 1185* (UKMB). **H.** *L. patriciae* Schäf.-Verw. from *G.E. Lee 1099* (UKMB).

Oil bodies. Generally, *Lejeunea* has small, finely granular and homogenous oil bodies. The number of oil bodies per cell and the shape of the oil bodies varies among the species in this genus, e.g., *L. lumbricoides* (Nees) Nees has more than 8 oil bodies per cell, usually ovoid, rarely ellipsoid, slightly glistening, whereas *L. eifrigii* Mizut. has less than 8 oil bodies per cell, normally 3–5 per cell, usually ellipsoid, sometimes ovoid, and opaque (Fig. 5). However, most of the species, e.g., *L. discreta* Lindenb. and *L. patriciae* Schäf.-Verw. have more than 8 oil bodies per cell, ovoid to ellipsoid, which are glistening to somewhat opaque.

Perianth. The perianth in most species has 5 keels. However, perianths without keels can also be found as in *L. albescens* (Steph.) Mizut., *L. cucullifiora* (Steph.) Mizut., *L. microloba* Taylor and *L. umbilicata* (Nees) Nees. The eplicate perianth is rather a widespread character in *Lejeunea.* Reiner-Drehwald and Schäfer-Verwimp (2008) treated 13 species of *Lejeunea* with eplicate perianth, occurring in America, Europe

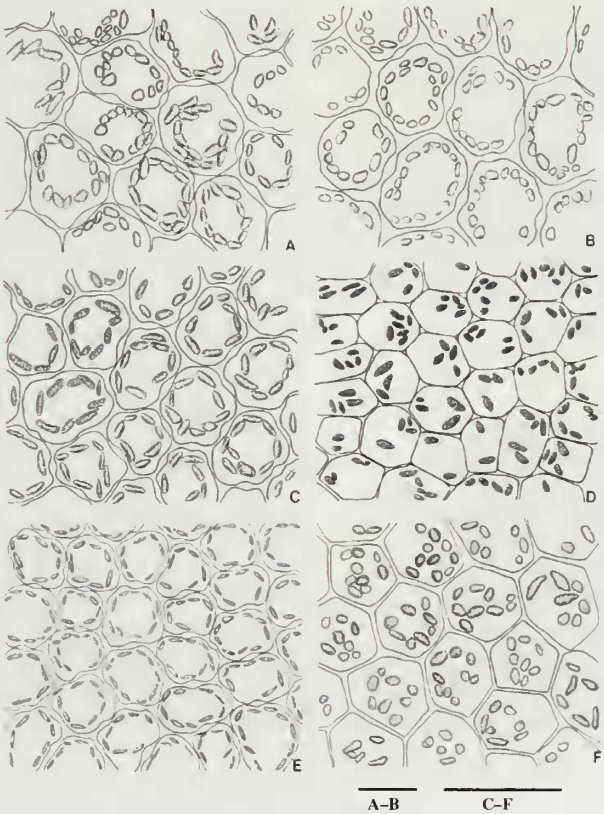

Fig. 5. Oil bodies. **A.** *L. patriciae* Schäf.-Verw. from *G.E. Lee 1099* (UKMB). **B.** *L. lumbricoides* (Nees) Nees from *G.E. Lee 1184* (UKMB). **C.** *L. discreta* Lindenb. from *G.E. Lee 1423* (UKMB). **D.** *L. eifrigii* Mizut. from *G.E. Lee 1194* (UKMB). **E.** *Lejeunea* sp. from *G.E. Lee 1424* (UKMB). **F.** *L. wightii* Lindenb. from *G.E. Lee 1423* (UKMB). Scale bars: A, B = 50 μm; C–F = 100 μm.

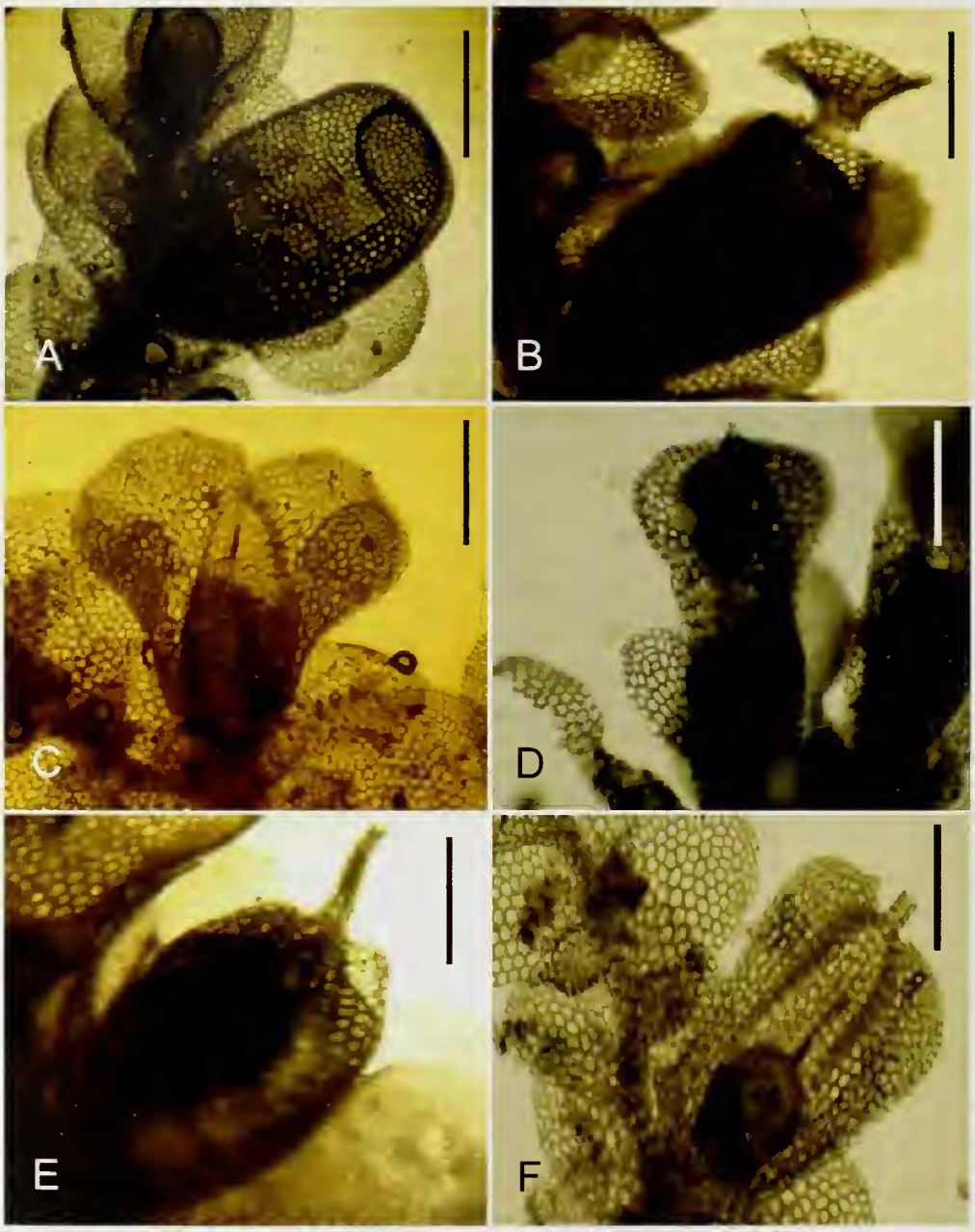

Fig. 6. The perianth of *Lejeunea*. **A.** *L. cucullifiora* (Steph.) Mizut. from *P.Y. Woug* with *Kim Wong 1604* (NICH). **B.** *L. minuula* Hürl. from *M. Mizutani 3239* (NICH). **C.** *L. papilionacea* Steph. from *Damanhuri s.n.* (UKMB). **D.** *L. eifrigii* Mizut. from *G.E. Lee 1185* (UKMB). **E.** *L. pectinella* from *Damanhuri s.n.* (UKMB). **F.** *L. anisophylla* Mont. from *G.E. Lee s.n.* (UKMB). Scale bars: A–F = 0.2 mm.

and Africa. The apex of the perianth also plays an important role in separating some of the taxa. A funnel-shaped apex is found only in *L. mimula* Hürl. and an apex with a 5–7-cells-long beak occurs only in *L. pectinella* Mizut. (Fig. 6).

Lobule with a large disc cell. In some species a large rectangular cell, called the disc cell by Mizutani (1970), very much larger than the first tooth, is situated below the first tooth (Fig. 1). Species with this peculiar character are *L. lumbricoides* (Nees) Nees and *L. discreta* Lindenb. Most species, however, lack such a large rectangular cell and sometimes this cell is of the same size as the first tooth, viz., in *L. albescens* (Steph.) Mizut., *L. microloba* Taylor, and *L. sordida* (Nees) Nees.

Underleaf with two large basal cells. This feature has been used to separate the species of *Lepidolejeunea* and *Luteolejeunea* by Piippo (1986). In the majority of *Lejeunea* species these two large basal cells are present and easily distinguished (Fig. 7). The presence of these two large basal cells was found in *L. lumbricoides* (Nees) Nees, *L. microloba* Taylor, *L. umbilicata* (Nees) Nees and *L. eifrigii* Mizut. but not in *L. sordida* (Nees) Nees where the two large basal cells are undistinguishable.

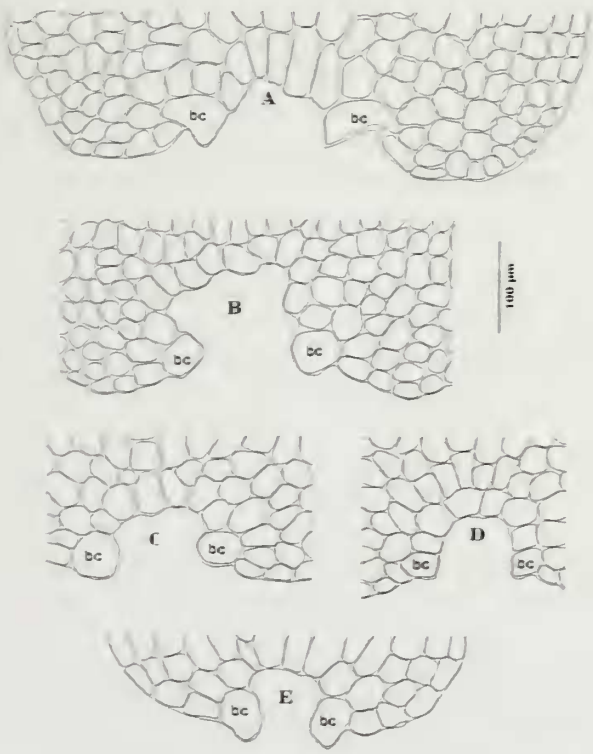

Fig. 7. Underleaf with two large basal cells (bc). **A.** *L. lumbricoides* (Nees) Nees from *G.E. Lee 1428* (UKMB). **B.** *L. microloba* Taylor from *Kodama 40783* (NICH). **C.** *L. umbilicata* (Nees) Nees from *M. Mizutani 3769* (NICH). **D.** *L. sordida* (Nees) Nees from *G.E. Lee 1231* (UKMB). **E.** *L. eifrigii* Mizut. from *G.E. Lee 1168* (UKMB).

Outlook

Our taxonomic study suggests that some species of *Lejeunea* are very similar and might lead to some new synonymy. For example, herbarium materials of *L. pectinella* Mizut. and *L. mizutanii* Grolle from Malaysia are very similar, *L. dipterocarpa* E.W. Jones from West Africa (Jones 1972), *L. hui* R.L. Zhu from China (Zhu & So 2001) and *L. kashyapii* M. Dey, D.K. Singh & D. Singh from India (Dey et al. 2008) are almost inseparable from *L. papilionacea* Steph. The last species was considered an African species but Söderström et al. (2010) have recently reported this species from Java where it was described as *Cardiolejeunea cadiantha* Schust. & Kachroo. If the above-mentioned species are indeed conspecific, it would seem that *L. papilionacea* Steph. is actually widespread in Asia. Furthermore, the difference between *L. wightii* Lindenb. and *L. tuberculosa* Steph., and between *L. cucullifiora* (Steph.) Mizut. and *L. umbilicata* (Nees) Nees, is probably not sufficient to warrant species distinction for these pairs of taxa. We are now trying to solve these problems by studying the type specimens and additional materials. We also expect that further new additions to Malaysia will be discovered in the future. Finally, we anticipate the separation of the genus *Microlejeunea* from *Lejeunea* and the treatment of the Asiatic *Lejeuna punctiformis* Taylor as a species of *Microlejeunea*. This species differs from *Lejeunea* species in the stem which has only 3 medullary cells in transverse section, leaf lobe with 1 or 2 ocelli at the base, a very large lobule, the first lobule tooth being rather long and curved, the keel of the female bracts winged and occasionally dentate female bracteoles. These characters also serve to separate *Microlejeunea* from *Lejeunea* (see, e.g., Bischler et al. (1962) for a thorough discussion of their differences).

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